

Biotic hotspots in mangrove-dominated estuaries: macro-invertebrate aggregation in unvegetated lower intertidal flats

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ABSTRACT: Macro-benthic invertebrates are important components of estuarine communities providing links between primary producers and higher trophic levels. In temperate regions, abundance and biomass peak in the mid-intertidal, giving this zone substantial functional importance. In tropical estuaries, the higher intertidal is generally occupied by mangrove forests, potentially influencing the way intertidal invertebrate assemblages are structured. We investigated the distribution and richness of benthic invertebrates across intertidal sand- and mud-flats seaward of mangrove forest to quantify the extent and location of areas of high benthic richness, abundance and biomass. Four estuaries in tropical north Queensland and 2 habitat types, sand and mud, were sampled using a van Veen grab. Macro-invertebrate richness, abundance and biomass peaked with a 'hotspot' in the lower low-intertidal, with patterns of distribution similar among substrate types. However, substantial differences in biotic and abiotic contexts between tropical estuaries and the temperate systems, where models of intertidal macro-invertebrate distribution were developed, mean that the variables influencing tropical macro-invertebrate hotspots are likely to differ from those that operate in temperate regions. The high concentration of benthic biomass in the lower low-intertidal means this zone probably regulates many of the ecological processes occurring in the intertidal regions of tropical estuaries. Consequently, any damage or modification to this zone is likely to severely impact estuarine function.

KEY WORDS: Benthos · Tropical estuary · Nutrients · Invertebrate distribution

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INTRODUCTION

Estuaries are among the most productive environments on earth (Beck et al. 2001, Vasconcelos et al. 2007), comprising a variety of habitats (saltmarsh, mangroves, seagrass, mud-flats, sand-flats, etc.), that together sustain high numbers of benthic and pelagic species (Kennish 2002, Wolanski 2014). Macro-benthic invertebrate communities are particularly important in estuaries because they are crucial components of food webs, providing vital conduits for the transfer of energy between primary producers and higher trophic levels (Tito de Moraes & Bodiou 1984, Coull

1990, Abrantes & Sheaves 2009, McPhee et al. 2015). Because macro-benthic invertebrates comprise a diversity of primary consumers, ranging from sub-surface and surface deposit feeders to filter feeders (Gaston et al. 2015), they are key agents in diversifying the ways in which energetic resources are made available to higher consumers (Hajisamae 2009, Davis et al. 2014).

Ecological studies investigating benthic distribution and composition in tropical estuaries have often focused on determining species composition and identifying the abiotic factors influencing a particular community (Kneib 1984, Alongi 1987, Vargas 1988,

Dittmann 2000), rather than on quantifying the ecological importance of the benthic community within a larger context. For instance, although we know from other ecosystems that strong gradients of change are common in intertidal macro-benthic assemblages (Connell 1972), we have little knowledge of how benthic communities change across different sub- and inter-tidal levels of tropical estuaries or among different estuarine reaches (Dittmann & Vargas 2001). Lack of this information has resulted in a poor understanding of the extent to which tropical benthic communities vary in their ecological roles and values. This is particularly important in light of the strong trophic links that produce well-defined relationships between invertebrate and fish abundances in tropical estuaries (Davis et al. 2014) and underpin the importance of estuaries as feeding grounds for juvenile nekton (Robertson & Duke 1990, Nagelkerken et al. 2000). The limited spatial extent of past studies exacerbates the problem; most studies of tropical estuarine benthos have focused on a single location, meaning there is insufficient information to allow observed patterns to be generalized to predict benthic community structure at other locations (Dittmann 2002).

Connell (1972) pioneered understanding of vertical zonation in ecological pattern and function of intertidal invertebrates. Using rocky shore environments, Connell (1972) developed a model describing the distribution of intertidal macro-benthic invertebrates as hump-shaped, with the highest biomass, taxonomic richness and abundance in the mid-intertidal, decreasing toward both higher and lower tidal limits. This model explains intertidal invertebrate distribution as limited by exposure (leading to desiccation) at the upper tidal limit and by predation in lower intertidal/subtidal areas. The peak in taxonomic richness observed in the mid-intertidal corresponds with high abundance and biomass, and so represents an important nutritional reservoir that can only be exploited for short periods by either aquatic (Menge 1976, Robles & Robb 1993) or terrestrial predators (Delibes et al. 2004).

In general, Connell's model has tacitly been assumed to apply to other intertidal situations; however, its reliability for tropical estuaries has yet to be established (Dittmann 2001). The shores of tropical estuaries are generally bordered by mangroves that occupy the upper intertidal limits of mud- and sand-flats (Alongi 2009). This abrupt change in habitat types (sand/mud in the lower intertidal to mangroves in the higher intertidal) means the intertidal comprises 2 distinct regions, making disjunct zonation inevitable at the whole-of-intertidal scale (Dittmann

2001). The inevitable faunal changes across these disjunct zones have substantial repercussions for nursery ground function, trophic transfer, nutrient subsidies, cross-intertidal connectivity and metacommunity interactions (Kneib 1997, Gillanders et al. 2003, Sheaves 2005, Nagelkerken et al. 2015). However, assuming a Connell-type model suggests there is likely to be additional zonation within each of these disjunct zones, adding further complexity to both faunal pattern and the way ecological interactions operate. For instance, a specific peak of invertebrate abundance within the lower half of the intertidal zone (in tropical estuaries the part of the intertidal below the mangrove line) represents a peak in prey abundance for invertebrate-feeding fish and therefore is likely to be a critical driver of the aggregation patterns of tropical estuarine fish that occur in greatest abundances along shallow intertidal banks (Johnston & Sheaves 2007, 2008). A corollary of this pattern is that these are also key areas where nutrients sequestered by invertebrates are uploaded into food webs via trophic transfer as well as bioturbation (Queirós et al. 2015). Consequently, understanding the distribution of benthic invertebrates within this zone is crucial if key ecological functions of tropical estuaries are to be understood and areas with higher benthic invertebrate biodiversity, biomass and abundance identified (i.e. hotspots).

We investigated macro-benthic invertebrate distribution and richness across sand and mud habitats of the low-intertidal zone of 4 estuaries in tropical north-eastern Australia to determine if they displayed 'Connell-type' humped distributions. Our objective was to build a detailed understanding of patterns of macroinvertebrate composition and abundance across low-intertidal and immediate adjacent subtidal estuarine habitats in order to identify biodiversity and nutrient up-load hotspots.

MATERIALS AND METHODS

Study sites

This study was conducted on the lower intertidal flats (i.e. seaward of the lower mangrove edge) and adjacent sub-tidal areas of 4 tropical estuaries of the north-east coast of Queensland, Australia (Fig. 1): 2 in the wet tropics (Hull River and Deluge Inlet), median annual rainfall 2062 mm (BoM 2013), and 2 in the dry tropics (Ross River and Yellow Gin Creek), median annual rainfall approximately 1050 mm (BoM 2013). All are mangrove-lined for most of their

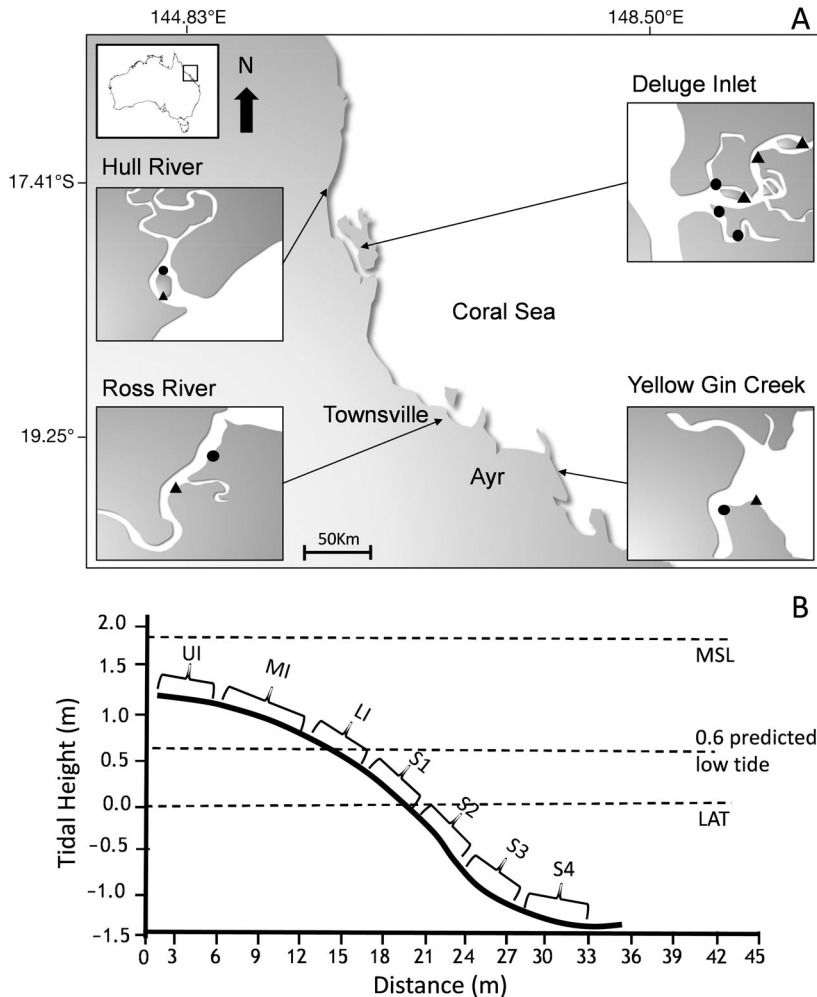


Fig. 1. (A) North-east coast of Australia showing the location of Hull River, Deluge Inlet, Ross River and Yellow Gin Creek, with insets indicating the sampled sites (circles = mud, triangles = sand). (B) Diagram of the sampling zones across the low-intertidal indicating the different tidal inundation levels (MSL: mean sea level, LAT: lower astronomical tide) with sampling zone identified (UI: upper low-intertidal, MI: mid low-intertidal, LI: lower low-intertidal, S1: Subtidal 1, S2: Subtidal 2, S3: Subtidal 3, S4: Subtidal 4)

lengths but their location in the wet tropics means that Deluge Inlet and the Hull River have higher taxonomic richness and density than the other 2 locations (Duke 2006).

The 4 locations were characterized by different degrees of anthropogenic influence. The most impacted were Yellow Gin Creek and Ross River. Yellow Gin Creek is partially surrounded by agricultural land devoted to sugarcane production and grazing (NRMW 2006). Ross River is situated in an urban-industrial area and so is influenced by a range of anthropogenic pressures that include contaminants from marinas, recreational and commercial boating, urban pollution and storm water and effluent discharges (Scheltinga & Heydon 2005). Hull River is a

largely unmodified estuary with little anthropogenic pressure, whereas Deluge Inlet is near pristine (Sheaves et al. 2014).

Because of its near-pristine condition, Deluge Inlet was chosen as an initial detailed study for the creation of a model of macro-benthic invertebrate distribution and richness. The resulting model was then evaluated in the other 3 estuaries.

Sampling techniques

Sampling was carried out in the dry season (June 2005 and 2006) and the wet season (February 2006) at Deluge Inlet, while model-evaluation estuaries were sampled once between February and June 2006. Data were collected at 6 sites within Deluge Inlet, half of which were characterized by sandy sediment and half by muddy sediment (Fig. 1). At the other 3 locations, 2 sites were sampled, one comprising each sediment type (Fig. 1).

A Van Veen grab (0.1 m^{-2}) was used to collect benthos and sediment samples, and organism abundance was then standardized into density for ease of comparison with previous studies (ind. m^{-2}). After measurement, samples were sieved through a 0.5 mm mesh and the retained material collected and stored in 10% buffered formalin. In the laboratory, samples were sorted to the lowest taxonomic level possible under a

stereo dissecting microscope, with subsequent identification assisted by use of high-power microscopy.

Sampling was conducted at different tidal levels based on their vertical height in the low-intertidal zone, between the lowest astronomical tide (LAT) level and the mangrove edge (approximately mid-low tide) (Duke 2006). These zones were classified as follows:

Upper low-intertidal (UI): the upper one third of the low-intertidal zone, the area immediately adjacent to the mangrove fringe; this zone was covered by the tide for only a few hours each day.

Mid low-intertidal (MI): the mid one third of the low-intertidal, vertically mid-way between the upper and lower low-intertidal zones.

Lower low-intertidal (LI): The lower one third of the intertidal zone, the area immediately above low tide water level (0.6 m predicted height in the area); this zone is exposed to the atmosphere for just a few hours each spring tidal cycle.

Subtidal 1 (S1): The area approximately 0.5 m below the LI. This zone is submerged most of the time; however, the largest spring low tides expose this zone for short periods.

Subtidal 2, Subtidal 3 and Subtidal 4 (S2, S3, and S4): The 3 subtidal sampling sites were positioned sequentially further from shore, with each subtidal zone approximately 3 m wide. These 3 zones are never exposed to the atmosphere.

Three replicate samples were collected within each tidal zone at each site.

The biomass of macro-benthic invertebrates (grams per wet weight) was determined using a Sartorius A2005 analytical balance, after blotting on filter paper for 10 min.

Grain size was determined by sieving 50 g of dried sediment through 2 mm, 1.40 mm, 1 mm, 710 μm , 500 μm , 350 μm , 250 μm , 177 μm , 125 μm , 88 μm and 63 μm stacked sieves. The sediment falling within each size fraction was then re-weighed.

Carbon-nitrogen-sulphur (CNS) combustion analysis was performed on approximately 50 g of sediment pre-treated with dilute hydrochloric acid (0.1 N) to remove any carbonates. The samples were then dried in an oven at 103°C, ground, homogenised and analysed using an Elemental VarioMax CNS Analyzer.

Physical samples were pooled to give one value for each of the tidal zones at both muddy and sandy sites.

Data analysis

The data for each variable (i.e. total density, total biomass, total taxonomic richness) were analysed using Univariate Classification and Regression Trees (CARTs), with seasons (Dry or Wet), the 7 tidal zones (UI, MI, LI, S1, S2, S3 and S4) and the 2 habitat types (mud vs. sand) as explanatory factors for each of the CARTs. *Brachyura* and *Anomura* crustaceans were removed from the analysis due to their low occurrences and abundances and their high mobility compared to other benthos. The CART models were conducted using R open source software (RCoreTeam 2015) employing the *rpart* package (Therneau et al. 2015). The models were fitted using 10-fold cross validation, and the final CART models were selected based on the 1 standard error criterion (the smallest

tree with cross validation error within 1 SE of the tree with minimum cross validation error).

A Venn diagram was constructed based on the species presence across the tidal gradient from the upper low-intertidal (UI) to the subtidal 2 (S2) zone and assessed whether the transition zone between 2 ecotones (i.e. intertidal and subtidal) could lead to a peak in abundance and richness due to the presence of species adapted to live in both environments. Subtidal zones 3 and 4 were not included to simplify the interpretation of the diagram and because their position along the tidal gradient was distant from the ecotone interface.

Multivariate regression tree analysis (mCART) (De'ath 2002), based on a Bray-Curtis distance, was performed for each estuary. The dependent variables were determined by pooling the individual species into major taxonomic groups (i.e. Order and Class), with only the taxa occurring in >5% of samples at all 4 estuaries included in analyses. Data were log + 1 transformed to down-weight the effect of extreme values. The explanatory factors were the 7 tidal zones and the habitat types. The multivariate regression tree analysis was conducted using R open source software (RCoreTeam 2015) employing the *mvpart* package (De'ath 2007). The models were fitted using 10-fold cross validation and the final mCART models selected based on the 1 standard error criterion.

Physical data were analysed with principal component analysis using Primer E (Clarke & Gorley 2006) after normalization to remove the effect of different scales of measurement.

RESULTS

Sediment characteristics

There was a clear differentiation in sediment characteristics between the fine sediment sites (muddy) and the coarse sediment sites (sandy) at all 4 estuaries (Fig. 2), with the exception of the upper low-intertidal zones at the sandy sites, which were similar in physical characteristics to the intertidal muddy sites. The intertidal zones (UI, MI and LI) tend to be separated from the subtidal ones (S1, S2, S3 and S4); however, the intensity and the gradient vary between estuaries. In addition, the presence of carbon, nitrogen and sulphur was higher at the fine sediment sites in all estuaries. The overall pattern of sediment composition and structure did not vary among the 4 estuaries, with sites in the highly impacted Ross River and Yellow Gin Creek having similar sediment com-

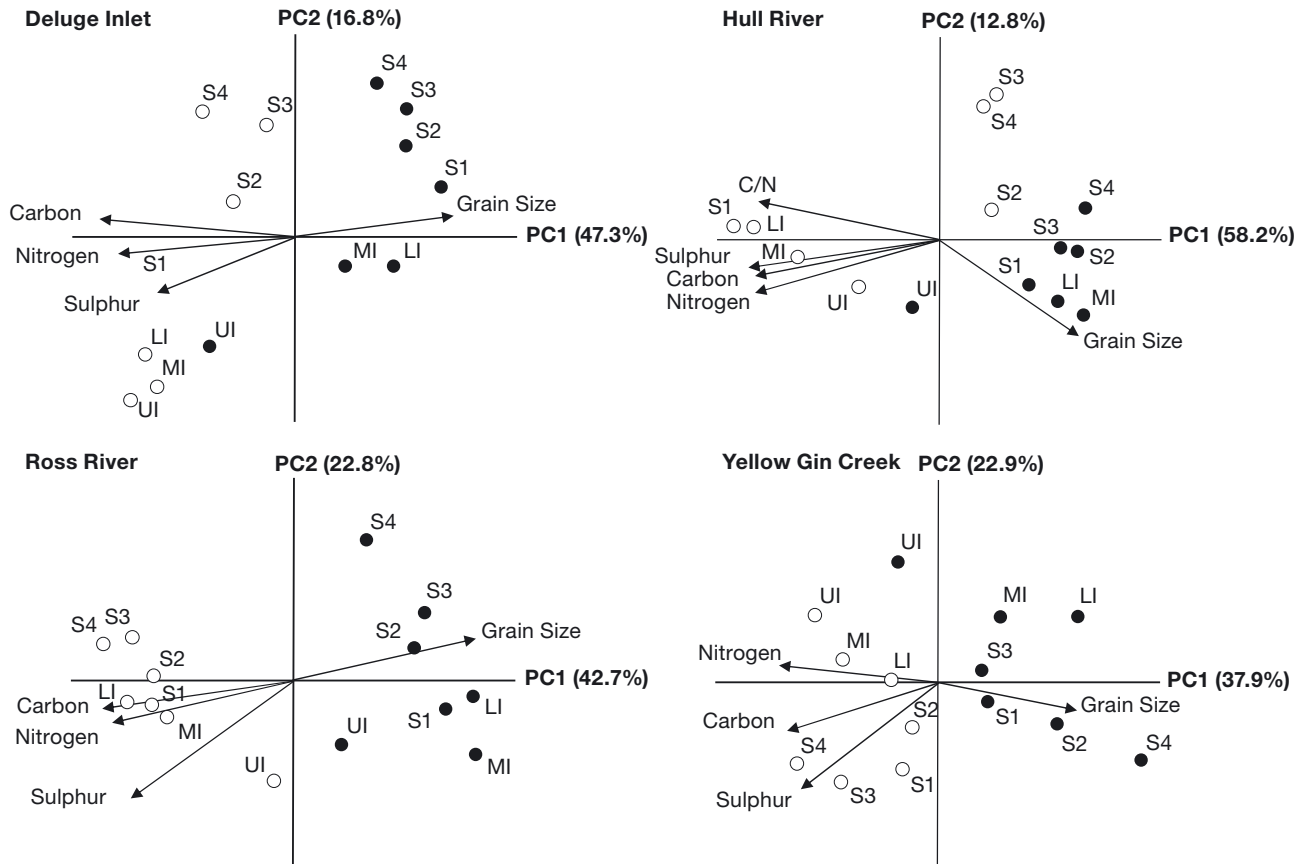


Fig. 2. Principal component analysis (PCA) for the ordination of the sediment composition at the 4 estuaries, sorted by site (filled circles = sand, empty circles = mud) and tidal zone (see Fig. 1 for abbreviations). The physical variables were superimposed on the ordination using loading vectors

positions to equivalent sites in the more pristine Deluge Inlet and Hull River.

Deluge Inlet benthic total density, biomass and taxonomic richness

The final CART models for total density, biomass and taxonomic richness at Deluge Inlet showed very similar results (Fig. 3), with samples differentiated by substrate type and tidal level. The model did not form viable splits based on season, indicating little influence of season on biomass, density and taxonomic richness. The total density (Fig. 3A) and biomass (Fig. 3B) of macro-benthic invertebrates both differed substantially between muddy and sandy sites, with the latter having overall higher densities, but both substrate types having the highest values in the LI and S1 zones. In contrast, for taxonomic richness, the primary split was by tidal zone, with intermediate tidal zones (MI, LI, S1) having a greater number of species regardless of the substrate type. Taxonomic

richness in the remaining tidal zones was strongly influenced by substrate type, with sandy substrates having higher taxonomic richness. Despite these minor differences, all 3 variables showed consistent overall patterns; in each case for both mud and sand estimates, the values of the CART terminal branches were highest in the uppermost subtidal level (S1), the lower low-intertidal level (LI) and sometimes in the slightly higher elevation of the mid low-Intertidal (MI), and then declined in lower subtidal and higher intertidal areas, clearly indicating humped-shaped distributions for all 3 variables. These hump-shaped distributions can be clearly seen across multiple variables for Deluge Inlet (Fig. 4), with lower total density, total biomass and taxonomic richness in the upper low-intertidal (UI) and deeper subtidal zones (S3, S4) and higher total density, total biomass and taxonomic richness in the intermediate zones. Highest values were concentrated in the LI (>30% of the total abundance and biomass). Furthermore, this pattern was constant for all sites and sediment compositions.

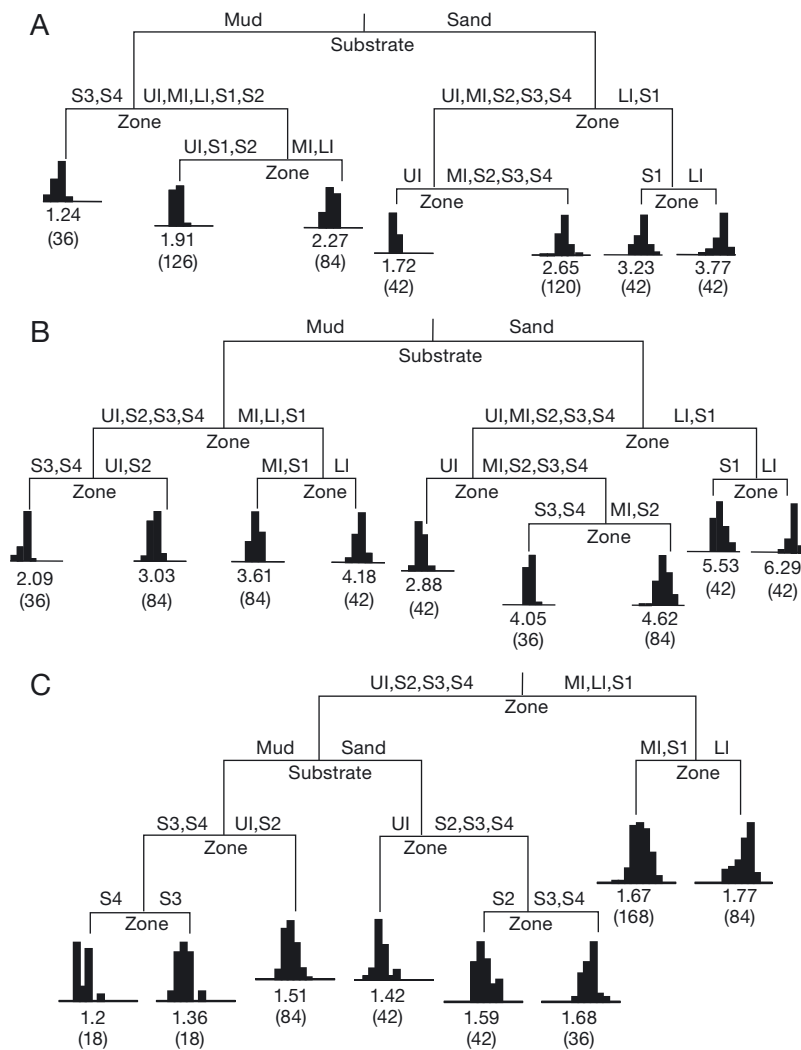


Fig. 3. Univariate regression tree (CART) for the proportion of (A) total density, (B) biomass and (C) taxonomic richness of macro-benthic invertebrates at Deluge Inlet (see Fig. 1 for abbreviations). Histograms represent frequency distributions of density, biomass or taxonomic richness at each terminal node. The numbers below represent the mean values, while the values in brackets represent the number of observations

The Venn diagram constructed to assess species occurrence across the tidal gradient (Fig. 5) shows zones differed in species composition and indicated little enhancement of abundance or richness due to the intertidal-subtidal ecotone. A total of 102 species were identified in the 5 zones (i.e. UI to S2), with nearly half the species found exclusively within 1 tidal zone. The intertidal had a total of 42 species that were not detected in the subtidal, while 29 species were only found in the subtidal, meaning that 31 species were observed in both the intertidal and subtidal zones. Just 2 species were found exclusively at the interface between 2 ecotones (i.e. LI and S1).

Comparison between Deluge Inlet and the other 3 estuaries

As with Deluge Inlet, the CARTs for the total density, biomass and taxonomic richness of macrobenthos at Hull River, Ross River and Yellow Gin Creek all showed highest values in the LI and immediate subtidal zones (S1) (Table 1). In contrast to Deluge Inlet, sediment type appeared to be less important in the other 3 estuaries, with substantial initial split determined by the tidal zones and estuary identity (see the Supplement at www.int-res.com/articles/suppl/m556p031_supp.pdf for details).

Invertebrate taxa across the four estuaries

Multivariate regression trees constructed using the 4 major taxonomic groups (Fig. 6A,C,E,G) confirmed the general trend of greater relative abundance/density in the lower low-intertidal (LI) and shallowest subtidal (S1) levels, with a generally bell-shaped distribution regardless of substrate type. There were strong differences in the relative contributions of the 4 taxonomic groups based on sediment type, with greater densities and higher taxonomic homogeneity in sandy substrates particularly evident in the intertidal regions (UI, MI and LI). Taxonomic structure varied between the 4 estuaries, especially in amphipod composition, with the 2 more impacted locations (i.e. Ross River and Yellow

Gin Creek) having extremely low densities regardless of sediment type and tidal location (Fig. 6A,C,E,G). Furthermore, regardless of sediment composition, the bell-shaped distribution for the 4 major taxa was more clearly defined at the more pristine sites. In particular, abundances of bivalves and gastropods were much more homogeneous across tidal levels at Ross River and Yellow Gin Creek (Fig. 6B,D,F,H). However, overall abundances were much higher at the 2 impacted estuaries, tending to flatten the hump-shaped distribution when the data are viewed in the log-transformed format needed to allow comparative visualisation of the 4 taxonomic groups.

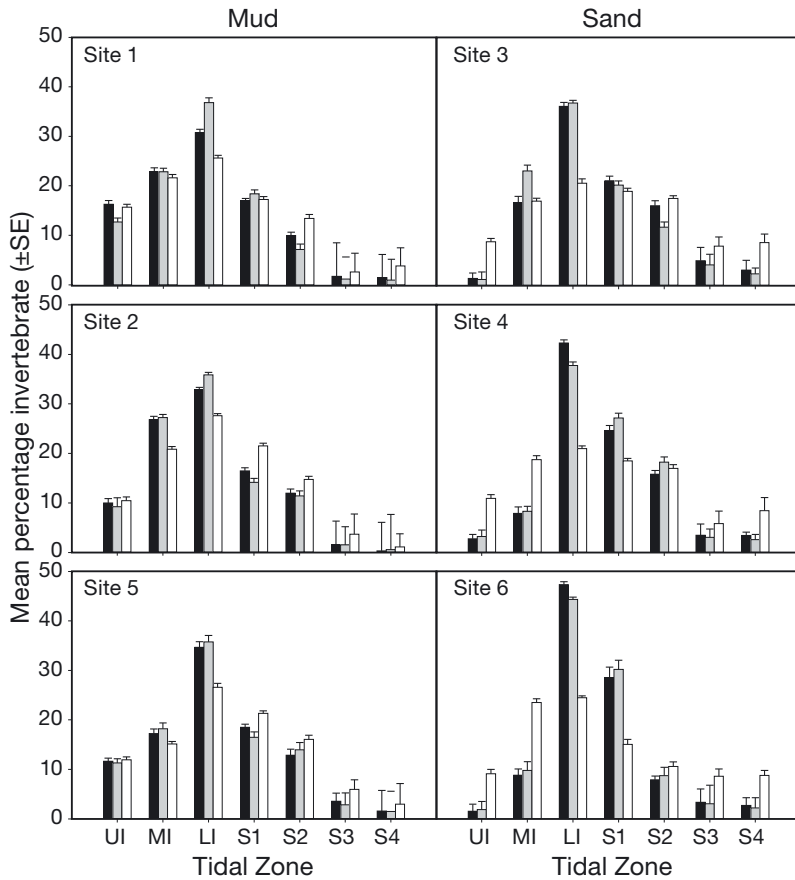


Fig. 4. Cross tidal pattern in the total density (black), biomass (grey) and taxonomic richness (white) of macro-benthic invertebrates at Deluge Inlet, separated by site, substrate type (i.e. mud and sand) and tidal gradient. See Fig. 1 for abbreviations

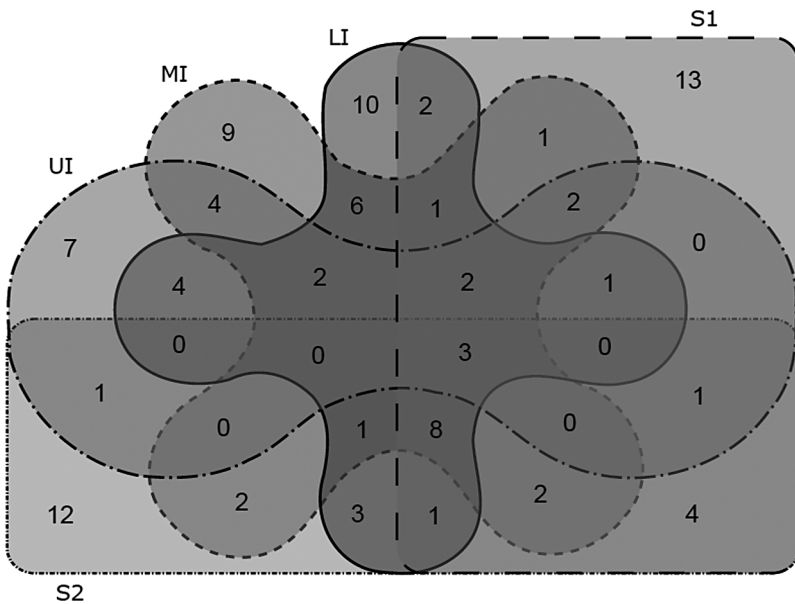


Fig. 5. Venn diagram describing the overlap in species occurrence across the various tidal zones (see Fig. 1 for abbreviations). Each tidal zone is identified by its abbreviation and corresponding unique outline style. The values and their position indicate the species overlap

DISCUSSION

Patterns of invertebrate distribution

The cross-tidal patterns for density, biomass and taxonomic richness of macrobenthos in the 4 estuaries all showed similar Connell-type hump-shaped distributions. Sediment characteristics are often associated with the distribution of benthic organisms; however, the humped shape distribution was observed across different sediment types (i.e. mud and sand), suggesting that position along the tidal gradient was more influential than sediment composition, a situation described for other habitats, such as beaches in Western Australia (Honkoop et al. 2006).

Although the general form of this distribution aligns with that seen in temperate areas (Connell 1972, Peterson 1991, Rodrigues et al. 2006, França et al. 2009), the location of the peak is different (Fig. 7), with the whole distribution defined within the lower half of the intertidal zone.

What factors might drive this difference? At least in part, the difference is probably attributable to fundamental differences between the systems; the original patterns for temperate areas were described from non-mangrove shores in areas with different climates, different tidal regimes and different suites of benthic invertebrates and predators. One obvious difference is the contrasting physical environment in the upper intertidal zone due to the presence of mangroves, both because of increased sediment organic content and because of shading from the mangroves. In fact, this does seem to be the case because a distinctly different fauna occurs in the mangrove zone (Dittmann 2001, Alfaro 2006). The mangrove fauna, however, is a low diversity, low abundance fauna (Dittmann 2001, Alfaro 2006) and so represents a tailing off of diversity, abundance and biomass, and thus the location of the

Table 1. Summary of the univariate regression trees of Deluge Inlet and the tested estuaries (Hull River, Ross River and Yellow Gin Creek) (see Supplement). The table shows the factors causing the first split in the tree and the zone that has the highest value

Dependent variable	Split information	Deluge Inlet	Test estuaries
Total density	1st node	Sediment	Tidal zones
	Highest value zones	Lower intertidal	Lower low-intertidal/Subtidal 1
Total biomass	1st node	Sediment	Tidal zones
	Highest value zones	Lower low-intertidal	Lower low-intertidal/Subtidal 1/Subtidal 2
Taxonomic richness	1st node	Tidal zones	Estuaries
	Highest value zones	Lower low-intertidal	Lower low-intertidal/Subtidal 1

Connell-type 'hump' in the lower low-intertidal zone needs further explanation.

Despite the obvious climatic and vegetation differences between tropical and temperate regions, the same underlying ecological processes that result in the general hump-shaped pattern in the intertidal benthic invertebrate distribution in temperate regions would be expected to drive distributions in the tropics.

Consequently, one possible explanation for peaks in benthos abundance and diversity is enhancement due to ecotone effects resulting from the occurrence of species within the ecotone that are capable of utilising habitats on both sides of the ecotone (Risser 1995, Lloyd et al. 2000). This is unlikely to be the case in the current situation; only 2 species were shared between the LI and the S1, and for both LI and S1, about one third of all species found there were exclusive to that zone.

More likely, as in temperate areas, the hump-shaped distribution pattern is likely to reflect the synergistic effects of abiotic and biotic factors. Tidal inundation duration and frequency influences how high in the tidal gradient marine organisms can colonize (Raimondi 1988). Prolonged exposure to higher temperatures and desiccation act as a physical barrier to occupancy depending on each species' tolerance (Sousa 1979, Vargas 1988, Peterson 1991). This effect is still likely to influence the ability of many marine invertebrates to colonise upper parts of intertidal sand- and mudflats, where greater exposure to the tropical sun makes these zones increasingly unsuitable for marine invertebrates. Consequently, differential tolerance to desiccation is likely to at least partially account for the upper tail of the hump-shaped distribution. In temperate systems, the benthic invertebrate distribution at the lower intertidal/subtidal limit is usually controlled by predation because the higher duration and frequency of inundation allow access to benthic-feeding fish and inver-

tebrates for longer periods, compared to the mid- and upper intertidal zones (Gilinsky 1984, Little 2000). It seems likely that predation would also limit the macro-benthic distribution in lower intertidal areas of tropical shores but perhaps in a more complex manner than in temperate ones. Slow-moving invertebrates, such as gastropods, other molluscs and sea stars, are the major macrobenthos predators in the studies from temperate regions used to formulate and confirm the models of the vertical distribution of invertebrates (Connell 1972, Gaines & Roughgarden 1985, Boaventura et al. 2002). In contrast, benthic feeding fish are the primary macrobenthos predators in tropical estuaries (Wilson & Sheaves 2001). These have a greater mobility than most macro-benthic invertebrate predators and so can penetrate throughout the intertidal to feed. Despite this higher mobility, the present study suggests that the feeding of benthivorous fish is heterogeneously distributed across the intertidal gradient, otherwise a flatter invertebrate distribution should have been observed. This makes sense because, unlike many invertebrate predators that possess adaptations (e.g. the protective shells of gastropods) allowing them to remain in the intertidal at low tide, most fish can only access the intertidal when it is flooded, meaning the duration of their feeding activities is determined by tidal flooding patterns (Baker et al. 2015). Many species of fish conduct horizontal migration into the intertidal areas to access areas of high food density (Gibson 2003). The exact pattern of utilisation depends on the species, size and life-history stage (Gibson 2003). For instance, smaller size fish are generally the first to access the intertidal during flooding tide and the last to leave, likely taking advantage of their lower water depth requirements (Giarrizzo et al. 2010). This behaviour gives the smaller fish the opportunity to feed undisturbed by larger fish, reducing competition for resources and predation risk (Wilson & Sheaves 2001, Giarrizzo et al. 2010).

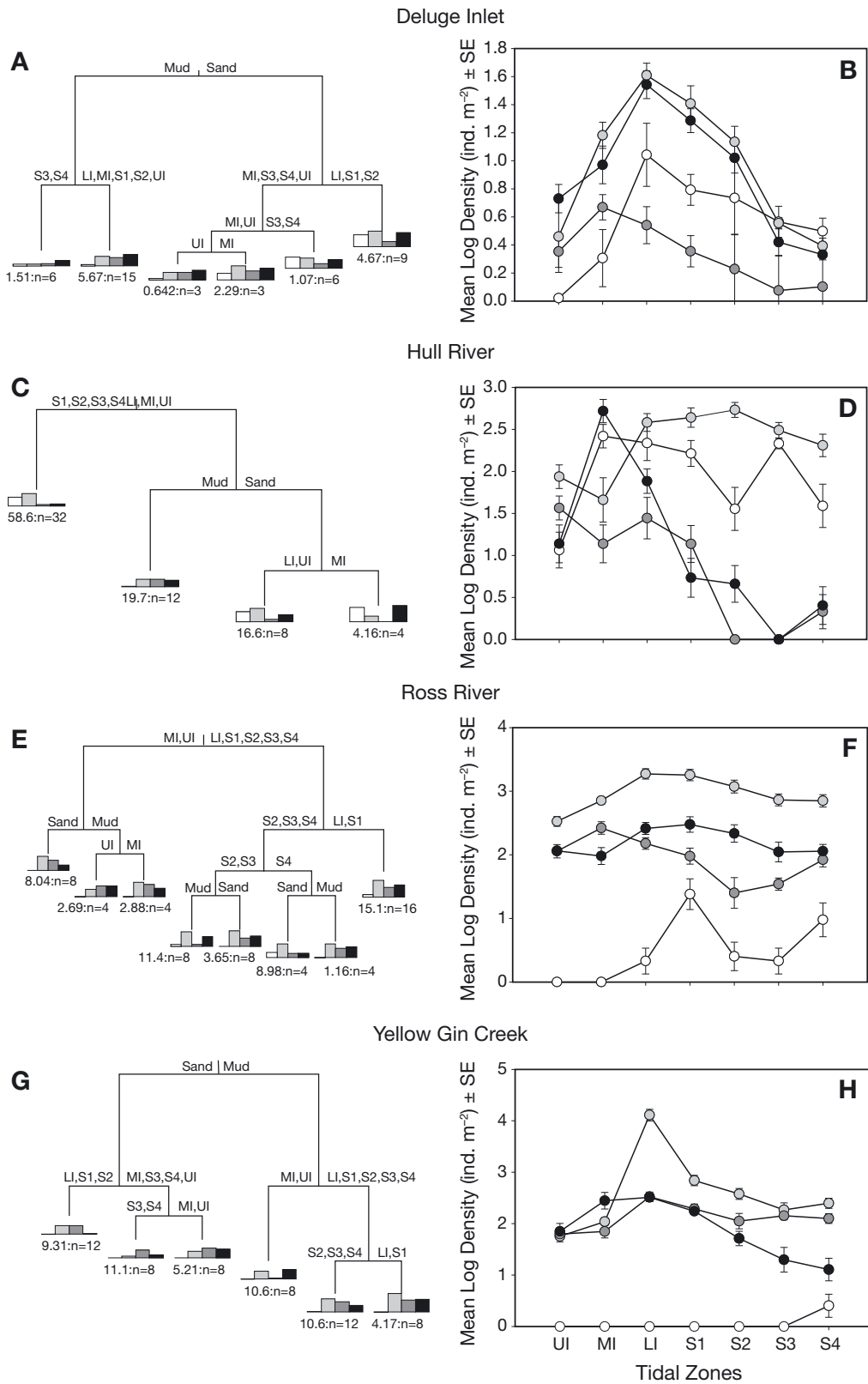


Fig. 6. Spatial distribution of the 4 most common groups of invertebrates (white: Amphipoda, light grey: Bivalvia, dark grey: Gastropoda, black: Polychaeta) across the tidal gradient (see Fig. 1 for abbreviations) at the 4 estuaries. Left: multivariate regression trees provide an indication of the relative abundance of each taxa at the various tidal zones (A: Deluge Inlet, C: Hull River, E: Ross River, G: Yellow Gin Creek). Values at each terminal node represent estimated mean and number of observations. Right: lineplots of the log₁₀ mean density of the 4 taxa provide a visual representation of the distribution pattern across the 7 tidal zones regardless of sediment type (B: Deluge Inlet, D: Hull River, F: Ross River, H: Yellow Gin Creek)

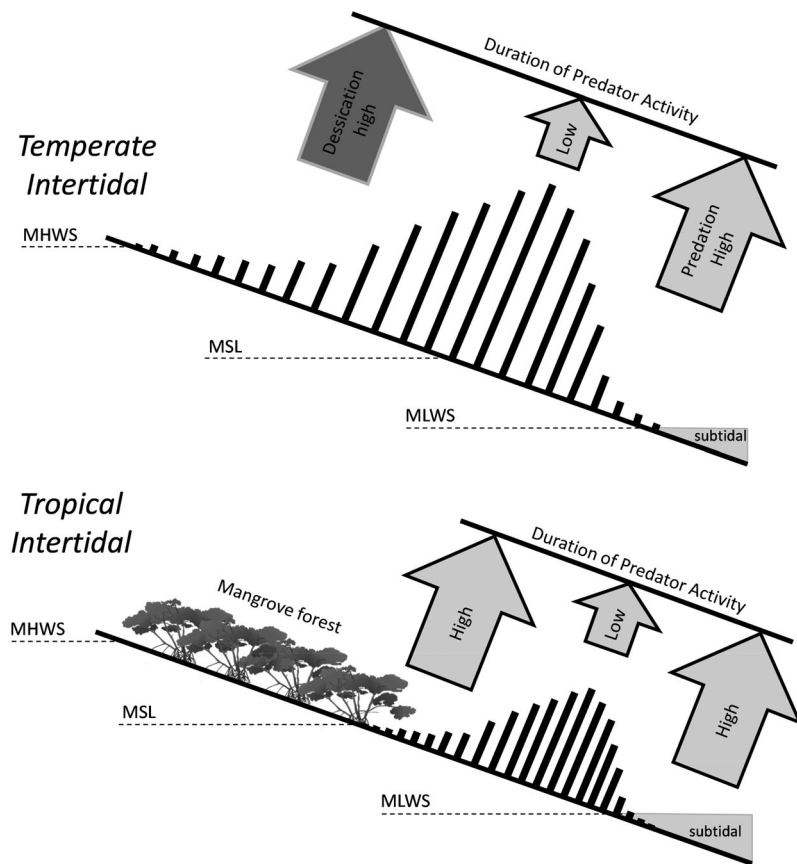


Fig. 7. Diagram of the proposed generalized distribution of macro-benthos along the tidal gradients of temperate (top) and tropical (bottom) regions (MHWS: Mean High Water Springs, MSL: Mean Sea Level, MLWS: Mean Low Water Springs). The size of the arrows represents the intensity of the disturbance. The bars represent the humped-shape distribution of the invertebrate fauna

The constant predation pressure on the subtidal zone (because it can always be accessed by marine predators) (Connell 1972, Little 2000) is the likely reason for low invertebrate densities, biomasses and different assemblage compositions there. Low prey availability in the subtidal means that benthic feeding fish need to move up with the tide to access richer intertidal feeding habitats. However, many benthivorous fish are small in size and find refuge from predation in the shallower water by following the tidal edge during flood tides (Wilson & Sheaves 2001). Such a tactic could result in a brief feeding periods in each zone of the lower intertidal, ending once water was too deep to provide refuge, and a second brief feeding opportunity during ebb tides. These restricted feeding opportunities would limit predation pressure on the lower intertidal areas. However, small benthivorous fish would still be able to feed for extended periods in the upper tidal gradient because the close proximity of mangroves would provide structural refuge for them to retreat

to when threatened by predatory fish (Robertson & Duke 1987, Laegds-gaard & Johnson 2001, Sheaves 2005). This would reinforce the hump-shaped distribution peak in the lower intertidal zone. At this stage, this explanation is based on the few studies available that have assessed the movements and feeding activities of fish across tropical intertidal zones, so further evaluation of potential explanation is needed. Such studies could take the form of more detailed assessment of the pattern of use of upper intertidal areas by small benthivorous fish, as well as investigation of patterns and rates of fish predation on juvenile fish across the intertidal. Predation by shorebirds is also potentially an additional factor explaining the humped-shaped distribution of invertebrates (Zou et al. 2008). However, shorebirds are usually only common on mangrove flats during seasonal migrations (Mercier & McNeil 1994), and, in fact, shorebird densities are almost invariably low on the mangrove flats of estuaries in the study area (M. S. pers. obs.).

Ecological consequences

The hump-shaped distribution of intertidal macro-benthos abundance, biomass and taxonomic richness in tropical estuaries has substantial ecological consequences because it means that the lower intertidal zone is a critical focus for a range of ecological processes. The presence of a substantial concentration of benthic prey biomass in the lower low-intertidal means that much of the integration of nutrition into higher tropic levels is likely to occur there, making it a hotspot for biological and biophysical processes and meaning that the condition of these habitats is likely to be critical to the health of the whole estuary.

The existence of a low-intertidal invertebrate hotspot is important in the context of food web dynamics and nutrient translocation. For instance, the highly diverse and abundant benthic community could enhance bioturbation when compared to adjacent zones, which would increase the organic nitrogen output to the whole estuary (Queirós et al. 2015).

Bioturbation is often considered to occur mostly within the rhizosphere; however, unvegetated areas, with a rich benthic community composition, can also support this process, actively enhancing the nutrient supply and regulating energy flows to other trophic groups (Bertics et al. 2010, Pillay et al. 2012).

Additionally, marine fish utilise rich intertidal feeding areas for only limited periods of the tide, so their tidal migrations transfer productivity from the lower intertidal to other estuarine habitats. At a more expansive scale, because many of the fish and invertebrates that use intertidal flats are juveniles of offshore species (Wilson & Sheaves 2001, Meynecke et al. 2008), they ultimately migrate to offshore adult habitats, transferring the energy gained in intertidal estuarine habitats to offshore ecosystems (McPhee et al. 2015, Sheaves et al. 2015). Similarly, intertidal nutrients are translocated to terrestrial habitats by birds that consume benthic invertebrates and small benthic feeding fish (Zou et al. 2008, Buelow & Sheaves 2015).

Beyond the translocation of intertidal productivity, there are implications for patterns of predation and nursery ground value. The need to access heterogeneously distributed resources means that fish must use a mosaic of habitats, a recognised characteristic of the use of estuaries by fish (Sheaves 2009, Berkström et al. 2012, França et al. 2012, Nagelkerken et al. 2015). In turn, the need to constantly move among habitats is a major driver for patterns of predation and predator avoidance in estuaries, where migrating fish are exposed to predation during inter-habitat movements (Sheaves 2009). Additionally, the aggregation of benthic prey in the lower low-intertidal makes it a vital area in nursery ground provisioning, one of the key roles of estuaries (Weinstein 1983, Weinstein et al. 2000, Beck et al. 2001).

The focussing of benthic biomass and ecological processes in the intertidal is also important in the context of patterns of human utilization and degradation of estuaries. Urban and industrial development around estuaries frequently modifies intertidal zones (Diaz 2001, Kennish 2002, Waltham & Sheaves 2015), creating the potential for substantial disruption of normal process that generate and maintain invertebrate hotspots. The central role of these areas in a range of ecosystem processes means that changes that result in the loss or modification of the benthic fauna will have far-reaching ecosystem consequences. However, there has been a tendency for evaluations of the value of estuarine habitats to focus on structurally complex habitats, such as mangroves and seagrass (e.g. Sheaves 1992, Dorenbosch et al.

2004), meaning there is a limited understanding of the value of unvegetated areas. As a result, it is common for estuarine modification to result in the loss of shallow sandy habitats and their replacement with unproductive deep water habitats (Waltham & Connolly 2013). Consequently, ignorance of the value of these habitats and their key role at a system scale threatens the values and ecosystem services of estuaries. This pattern of modification is repeated around the world (Waltham & Connolly 2011), making the undervaluing of benthic habitats a problem of global concern.

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LITERATURE CITED

- Abrantes KT, Sheaves M (2009) Food web structure in a near-pristine mangrove area of the Australian Wet Tropics. *Estuar Coast Shelf Sci* 82:597–607
- Alfaro AC (2006) Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. *Estuar Coast Shelf Sci* 66:97–110
- Alongi DM (1987) Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. *Mar Biol* 95: 447–458
- Alongi DM (2009) *The energetics of mangrove forests*. Springer Science & Business Media, New York, NY
- Baker R, Sheaves M, Johnston R (2015) Geographic variation in mangrove flooding and accessibility for fishes and nektonic crustaceans. *Hydrobiologia* 762:1–14
- Beck MW, Heck KL, Able KW, Childers DL and others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641
- Berkström C, Gullström M, Lindborg R, Mwandya AW, Yahya SAS, Kautsky N, Nyström M (2012) Exploring 'knowns' and 'unknowns' in tropical seascape connectivity with insights from East African coral reefs. *Estuar Coast Shelf Sci* 107:1–21
- Bertics VJ, Sohm JA, Treude T, Chow CET, Capone DC, Fuhrman JA, Ziebis W (2010) Burrowing deeper into benthic nitrogen cycling: the impact of bioturbation on nitrogen fixation coupled to sulfate reduction. *Mar Ecol Prog Ser* 409:1–15
- Boaventura D, Ré P, Cancela da Fonseca L, Hawkins SJ (2002) Intertidal rocky shore communities of the continental Portuguese coast: analysis of distribution patterns. *Mar Ecol (Berl)* 23:69–90
- BoM (2013) Australian Government Bureau of Meteorology, Climate Data Online. www.bom.gov.au/climate/data/
- Buelow C, Sheaves M (2015) A birds-eye view of biological connectivity in mangrove systems. *Estuar Coast Shelf Sci* 152:33–43
- Clarke K, Gorley R (2006) *User manual/tutorial*. Primer-E, Plymouth

- Connell JH (1972) Community interactions on marine rocky intertidal shores. *Annu Rev Ecol Syst* 3:169–192
- Coull BC (1990) Are members of the meiofauna food for higher trophic levels? *Trans Am Microsc Soc* 109:233–246
- Davis B, Mattone C, Sheaves M (2014) Bottom-up control regulates patterns of fish connectivity and assemblage structure in coastal wetlands. *Mar Ecol Prog Ser* 500: 175–186
- De'ath G (2002) Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology* 83:1105–1117
- De'ath G (2007) mvpart: multivariate partitioning. R package version 1.2-6. <https://cran.r-project.org/src/contrib/Archive/mvpart/>
- Delibes M, Clavero M, Prenda J, del Carmen Blázquez M, Ferreras P (2004) Potential impact of an exotic mammal on rocky intertidal communities of northwestern Spain. *Biol Invasions* 6:213–219
- Diaz RJ (2001) Overview of hypoxia around the world. *J Environ Qual* 30:275–281
- Dittmann S (2000) Zonation of benthic communities in a tropical tidal flat of north-east Australia. *J Sea Res* 43:33–51
- Dittmann S (2001) Abundance and distribution of small infauna in mangroves of Missionary Bay, North Queensland, Australia. *Rev Biol Trop* 49:535–544
- Dittmann S (2002) Benthic fauna in tropical tidal flats—a comparative perspective. *Wetlands Ecol Manage* 10: 189–195
- Dittmann S, Vargas J (2001) Tropical tidal flat benthos compared between Australia and Central America. In: Reise K (ed) *Ecological comparisons of sedimentary shores*. Springer, Berlin, p 275–293
- Dorenbosch M, Van Riel MC, Nagelkerken I, Van der Velde G (2004) The relationship of reef fish densities to the proximity of mangrove and seagrass nurseries. *Estuar Coast Shelf Sci* 60:37–48
- Duke NC (2006) *Australia's mangroves: the authoritative guide to Australia's mangrove plants*. University of Queensland, Brisbane
- França S, Vinagre C, Pardal MA, Cabral HN (2009) Spatial and temporal patterns of benthic invertebrates in the Tagus estuary, Portugal: comparison between subtidal and an intertidal mudflat. *Sci Mar* 73:307–318
- França S, Vasconcelos RP, Fonseca VF, Tanner SE, Reis-Santos P, Costa MJ, Cabral HN (2012) Predicting fish community properties within estuaries: influence of habitat type and other environmental features. *Estuar Coast Shelf Sci* 107:22–31
- Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc Natl Acad Sci USA* 82:3707–3711
- Gaston GR, Brown SS, Rakocinski CF, Heard RW, Summers JK (2015) Trophic structure of macro-benthic communities in northern Gulf of Mexico estuaries. *Gulf Caribb Res* 9:111–116
- Giarrizzo T, Krumme U, Wosniok W (2010) Size-structured migration and feeding patterns in the banded puffer fish *Colomesus psittacus* (Tetraodontidae) from north Brazilian mangrove creeks. *Mar Ecol Prog Ser* 419:157–170
- Gibson R (2003) Go with the flow: tidal migration in marine animals. *Hydrobiologia* 503:153–161
- Gilinsky E (1984) The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65:455–468
- Gillanders B, Able K, Brown J, Eggleston D, Sheridan P (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Mar Ecol Prog Ser* 247:281–295
- Hajisamae S (2009) Trophic ecology of bottom fishes assemblage along coastal areas of Thailand. *Estuar Coast Shelf Sci* 82:503–514
- Honkoop PJC, Pearson GB, Lavaleye MSS, Piersma T (2006) Spatial variation of the intertidal sediments and macro-zoo-benthic assemblages along Eighty-mile Beach, north-western Australia. *J Sea Res* 55:278–291
- Johnston R, Sheaves M (2007) Small fish and crustaceans demonstrate a preference for particular small-scale habitats when mangrove forests are not accessible. *J Exp Mar Biol Ecol* 353:164–179
- Johnston R, Sheaves M (2008) Cross-channel distribution of small fish in tropical and subtropical coastal wetlands is trophic-, taxonomic-, and wetland depth-dependent. *Mar Ecol Prog Ser* 357:255–270
- Kennish MJ (2002) Environmental threats and environmental future of estuaries. *Environ Conserv* 29:78–107
- Kneib R (1984) Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. *Estuaries* 7:392–412
- Kneib RT (1997) The role of tidal marshes in the ecology of estuarine nekton. *Oceanogr Mar Biol Annu Rev* 35: 163–220
- Laegdsgaard P, Johnson C (2001) Why do juvenile fish utilise mangrove habitats? *J Exp Mar Biol Ecol* 257:229–253
- Little C (2000) *The biology of soft shores and estuaries*. Oxford University Press, Oxford
- Lloyd KM, McQueen AAM, Lee BJ, Wilson RCB, Walker S, Wilson JB (2000) Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. *J Veg Sci* 11:903–910
- McPhee JJ, Platell ME, Schreider MJ (2015) Trophic relay and prey switching—a stomach contents and calorimetric investigation of an ambassid fish and their saltmarsh prey. *Estuar Coast Shelf Sci* 167:67–74
- Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol Monogr* 46:355–393
- Mercier F, McNeil R (1994) Seasonal variations in intertidal density of invertebrate prey in a tropical lagoon and effects of shorebird predation. *Can J Zool* 72:1755–1763
- Meynecke JO, Lee SY, Duke N (2008) Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. *Biol Conserv* 141:981–996
- Nagelkerken I, Van der Velde G, Gorissen M, Meijer G, Van't Hof T, Den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuar Coast Shelf Sci* 51:31–44
- Nagelkerken I, Sheaves M, Baker R, Connolly RM (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish Fish* 16:362–371
- NRMW (2006) *Burdekin Basin Draft Water Resource Plan Environmental Assessment Report: Phase III environmental implications of possible future water resource management scenarios*. Queensland Government, Brisbane
- Peterson CH (1991) Intertidal zonation of marine inverte-

- brates in sand and mud. *Am Sci* 79:236–249
- Pillay D, Williams C, Whitfield AK (2012) Indirect effects of bioturbation by the burrowing sandprawn *Callichirus kraussi* on a benthic foraging fish, *Liza richardsonii*. *Mar Ecol Prog Ser* 453:151–158
 - Queirós AM, Stephens N, Cook R, Ravaglioli C and others (2015) Can benthic community structure be used to predict the process of bioturbation in real ecosystems? *Prog Oceanogr* 137:559–569
 - Raimondi PT (1988) Settlement cues and determination of the vertical limit of an intertidal barnacle. *Ecology* 69:400–407
 - RCore Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
 - Risser PG (1995) The status of the science examining ecotones. *Bioscience* 45:318–325
 - Robertson A, Duke N (1987) Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other near-shore habitats in tropical Australia. *Mar Biol* 96:193–205
 - Robertson A, Duke N (1990) Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. *Mar Biol* 104:369–379
 - Robles C, Robb J (1993) Varied carnivore effects and the prevalence of intertidal algal turfs. *J Exp Mar Biol Ecol* 166:65–91
 - Rodrigues A, Meireles SN, Pereira T, Gama A, Quintino V (2006) Spatial patterns of benthic macro-invertebrates in intertidal areas of a southern European estuary: the Tagus, Portugal. *Hydrobiologia* 555:99–113
 - Schellinga D, Heydon L (2005) Report on the condition of estuarine, coastal and marine resources of the Burdekin dry tropics region. CRC for Coastal Zone, Estuary and Waterway Management, Indooroopilly. www.ozcoasts.gov.au/pdf/CRC/Burdekin_Coastal_Report_final_revised_screen.pdf
 - Sheaves MJ (1992) Patterns of distribution and abundance of fishes in different habitats of a mangrove-lined tropical estuary, as determined by fish trapping. *Mar Freshw Res* 43:1461–1479
 - Sheaves M (2005) Nature and consequences of biological connectivity in mangrove systems. *Mar Ecol Prog Ser* 302:293–305
 - Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. *Mar Ecol Prog Ser* 391:107–115
 - Sheaves M, Abrantes KG, Johnston R (2014) Deluge inlet, a pristine small tropical estuary in north-eastern Australia. In: Wolanski E (ed) *Estuaries of Australia in 2050 and beyond*. Springer, Dordrecht, p 261–275
 - Sheaves M, Baker R, Nagelkerken I, Connolly RM (2015) True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. *Estuaries Coasts* 38:401–414
 - Sousa WP (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239
 - Therneau T, Atkinson B, Ripley B (2015) rpart: recursive partitioning and regression trees. R package version 4.1-10. <https://cran.r-project.org/web/packages/rpart/index.html>
 - Tito de Morais L, Bodiou JY (1984) Predation on meiofauna by juvenile fish in a Western Mediterranean flatfish nursery ground. *Mar Biol* 82:209–215
 - Vargas JA (1988) A survey of the meiofauna of an Eastern Tropical Pacific intertidal mud flat. *Rev Biol Trop* 36:541–544
 - Vasconcelos RP, Reis-Santos P, Fonseca V, Maia A and others (2007) Assessing anthropogenic pressures on estuarine fish nurseries along the Portuguese coast: a multi-metric index and conceptual approach. *Sci Total Environ* 374:199–215
 - Waltham NJ, Connolly RM (2011) Global extent and distribution of artificial, residential waterways in estuaries. *Estuar Coast Shelf Sci* 94:192–197
 - Waltham NJ, Connolly RM (2013) Artificial tidal lakes: built for humans, home for fish. *Ecol Eng* 60:414–420
 - Waltham NJ, Sheaves M (2015) Expanding urban and industrial development in tropical seascapes necessitates green engineering and spatial planning thinking. *Environ Sci Technol* 49:2598–2599
 - Weinstein MP (1983) Population dynamics of an estuarine-dependent fish, the spot (*Leiostomus xanthurus*), Along a tidal creek-seagrass meadow coenocline. *Can J Fish Aquat Sci* 40:1633–1638
 - Weinstein MP, Litvin SY, Bosley KL, Fuller CM, Wainright SC (2000) The role of tidal salt marsh as an energy source for marine transient and resident finfishes: a stable isotope approach. *Trans Am Fish Soc* 129:797–810
 - Wilson J, Sheaves M (2001) Short-term temporal variations in taxonomic composition and trophic structure of a tropical estuarine fish assemblage. *Mar Biol* 139:787–796
 - Wolanski E (2014) *Estuaries of Australia in 2050 and beyond*. Springer, Dordrecht
 - Zou F, Zhang H, Dahmer T, Yang Q, Cai J, Zhang W, Liang C (2008) The effects of benthos and wetland area on shorebird abundance and species richness in coastal mangrove wetlands of Leizhou Peninsula, China. *For Ecol Manage* 255:3813–3818

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